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Title	A FIFTH SPECIES OF CHIONANDASPIS, WITH REFERENCE TO THE SIGNIFICANCE OF MONOTYPIC GENERA (STERNORRHYNCHA: COCCOIDEA: DIASPIDIAE)
Author(s)	Takagi, Sadao
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A FIFTH SPECIES OF CHIONANDASPIS, WITH REFERENCE TO THE SIGNIFICANCE OF MONOTYPIC GENERA (STERNORRHYNCHA: COCCOIDEA: DIASPIDIDAE)

By Sadao Takagi

Abstract

Takagi, S., 2008. A fifth species of *Chionandaspis*, with reference to the significance of monotypic genera (Sternorrhyncha: Coccoidea: Diaspididae). *Ins. matsum. n. s*. 64: 117–126, 1 fig.

Chionandaspis glutae, sp. nov., of which the female burrows into the leaf epidermis of *Gluta elegans*, is described from Penang Island, Malaya, Malaysia. Among the five known species of the genus, *C. glutae* is the most derivative in having fused median trullae in the adult and second-instar females, which are, thus, highly adapted to burrowing. *Chionandaspis* as a whole is a peculiar genus composed of burrowing species, but includes a less peculiar species, *C.* 91Kc-H. Starting with this species, some characters in the adult females change in succession through the five species. Other characters show a gap between *C.* 91Kc-H and the other species and another gap between the twig-inhabiting *C. ramicola* and the leaf-associated *C. foliicola*, *C. palawanensis*, and *C. glutae*. The known species of the genus represent a primitive form associated with the twigs and derivative forms differentiated in adaptation to the burrowing mode of life on the twigs and on the leaves. Many genera have recently been erected for isolated species of burrowing diaspidids, whereas monotypic genera remain problematical. *Chionandaspis* shows that even peculiar genera may arise with less peculiar species and, once established, may promote adaptive speciation. If this generalization is adopted, the problem of monotypic genera may be concerned with the dimensions of the adaptive zones they exploit rather than with their morphological peculiarities or the mechanisms by which they emerge.

Author's address. c/o Systematic Entomology, Graduate School of Agriculture, Hokkaidô University, Sapporo, 060-8589 Japan.

Contents. Introduction — Genus *Chionandaspis* — *Chionandaspis glutae*, sp. nov. — Discussion (Peculiar morphologies — Morphoclinal analyses — Ancestral form — Adaptive diversification — Gaps: saltatory changes?) — Concluding remarks — References — Figure.

Systematic and Ecological Surveys on Some Plant-parasitic Microarthropods in Southeast Asia, Scientific Report.

In my repeated trips in tropical Asia I concentrated on collecting scale insects in natural vegetation, and obtained a large amount of scale insect material, in which a great number of species, mainly of the family Diaspididae, have been found. My published papers still cover a smaller part of this collection, but it can be assumed from the collection that a rich diaspidid fauna, composed of diverse forms and remaining largely unknown, exists on wild plants in tropical Asia.

In studying the collection, I often came across isolated species, which required monobasic genera. In 2003, for example, I proposed 14 new genera for 16 species showing peculiar morphological characters, which are probably associated with their habit of burrowing into plant epidermal tissues, and thus I erected thirteen of these genera on the basis of single species. In principle, however, genera and other higher taxa are groups of species. These groups, recognized on the basis of discontinuities among morphological patterns, should have some definite biological significance. In a view—gradistic it may be called—taxa should reflect stasis and higher taxa should correspond to relatively stabilized anagenetic levels at which speciation takes place. 'Indeed, the facts of stasigenesis vouch for the non-arbitrary nature of gradal units' (Huxley, 1958), and this non-arbitrariness alone may verify the reality of taxa. On this understanding of evolution and taxa, monobasic higher taxa are problematical: are they really monotypic and, if they are, what do they mean?

'In botany the predominance of monotypic genera in groups from algae to angiosperms seems to have been accepted for years. … The characters that define these monotypic genera represent fundamental differences, and further study only adds more evidence of their uniqueness. In plants some monotypy may result from polyploidy. However, monotypy is found in numerous sexually reproducing plant and animal groups as well. … In bryozoans, for example, where understanding of genera is quite good, there are many monotypical genera and only a few genera that are really speciose' (Winston, 1999).

'The tropical rain forest harbours an unusually large number of isolated species and an impressive number of unusual structures. Many of these are taxonomic parallels of terata and all can be derived from growth phenomena' (Steenis, 1969). In plants, according to Steenis, teratological monstrosities are 'the most important means of macro-evolution by single large steps', leading to saltatory non-adaptive emergence of isolated species or monotypic genera.

In scale insects little has been discussed on monotypy and also on teratology. Monobasic genera have been described in the Diaspididae. In the present state of diaspidid taxonomy, however, it is impossible to know how many genera of the family are really monotypic.

My surveys in tropical Asia were too restricted in area and duration, and yet I have had the opportunities to add new species found in my collection to some genera that had long been represented by their type species alone. The view may be plausible, therefore, that many if not all monobasic diaspidid genera simply mean insufficient surveys. However, because monotypic genera are not unusual in some other groups of organisms (including the Bryozoa, which are, in general, sessile animals like the Diaspididae and represented by abundant paleontological as well as neontological material), the possibility that a good number of monotypic diaspidid genera exist especially under

tropical conditions should not be rejected.

Among the 14 genera I erected in 2003, only one, *Chionandaspis*, was not monobasic, comprising three species, *C. ramicola*, *C. foliicola*, and *C. palawanensis*. The genus was referred to the subtribe Chionaspidina, tribe Diaspidini, especially on the basis of the second-instar males of *C. ramicola* and *C. foliicola*. Later, another species was tentatively referred to the genus; it was not formally named but tagged '*C.* 91Kc-H' owing to the inadequate condition of the single specimen available of the adult female (Takagi, 2005). In the present paper a new species, *C. glutae*, is added to the genus. Examinations on these five species may give some insight into the evolution of such scale insects as burrowing forms with peculiar morphologies, and also into the significance of isolated species or monotypic genera.

Genus *Chionandaspis*

The localities and host plants of the five species recognized as members of this genus are as follows:
A) Species with the female burrowing into the twig epidermis.

Chionandaspis ramicola (type species). Santubong, Sarawak, Borneo Island, on *Swintonia glauca* (Anacardiaceae).

Chionandaspis 91Kc-H. Kuching, Sarawak, Borneo Island, on *Hopea* sp. (Dipterocarpaceae).
B) Species with the female burrowing into the leaf epidermis.

Chionandaspis foliicola. Santubong, Sarawak, Borneo Island, on *Swintonia glauca* (Anacardiaceae).

Chionandaspis palawanensis. Brooke's Point, Palawan Island, on *Antiaris toxicaria* (Moraceae).

Chionandaspis glutae, sp. nov. Penang Island, on *Gluta elegans* (Anacardiaceae).

C. ramicola and *C. foliicola*, occurring at the same locality on the same plant species, are distinguishable not only in the adult females, which differ in the burrowing sites, but also in the second-instar males, which occur on the leaves in both species. The new species definitely belongs to the genus. The unnamed species, *C.* 91Kc-H, is referable to the genus on the supposition that it represents a primitive form in the genus as will be discussed later.

The adult and second-instar females occur under a thin upper epidermal layer of the twigs or leaves. (In the three species originally referred to the genus and the new species, the female specimens were actually taken from under the covering epidermal layer; in *C.* 91Kc-H, the adult female specimen obtained was assumed to have been burrowing: see Takagi, 2005). In general, burrowing scale insects are not always easy to find in the field. *C.* 91Kc-H and the new species were found incidentally in the laboratory when other diaspidids were treated for mounting. It is not unreasonable, therefore, to expect that not a few unknown species of the genus exist in tropical Asia.

Chionandaspis glutae, sp. nov.

Material examined. Collected on Bukit Cendana [Chendana Hill], Pulau Pinang [Penang Island], Malaya, Malaysia, on *Gluta elegans* (Anacardiaceae; identified by K. M. Kochummen, Forest Research Institute of Malaysia), 16.XI.1991 [Material No.: 91ML-423]. Females occurring

on the lower surface of the leaf, burrowing into the leaf blade just beside the midrib or other veins. The burrow is visible through a transparent upper epidermal layer of the leaf, showing a white patch within, which should be secreted wax or the test. At a glance it appeared to be a mere discoloured point on the leaf, and the presence of this species on the plant material had not been noticed until an *Aulacaspis* species occurring on the same plant material was treated for mounting. Four specimens of the adult female, with their exuvial casts of the second instar, were mounted.

Holotype (adult female): deposited in the collection of Entomology Division, Forest Research Institute of Malaysia, Kepong, Kuala Lumpur.

Adult female. Body elongate, frontal margin flat, meso- and metathorax slightly and abd I–III [first to third abdominal segments] moderately lobed laterally; pygidium obdeltate, with lateral margins straight. Prepygidial derm membranous; a tubercular eye-spot on each side of prosoma somewhat anteriorly to the level of the anterior spiracle; a small inconspicuous prominence on lateral margin of mesothorax, bearing 3 setae; a prominent digitiform prominence on lateral lobe of metathorax, with 3 setae; a submarginal dorsal boss on abd I; pygidium not strongly sclerotized dorsally, ventral surface with a sclerotized aliform patch in front of median trullae. Antennae near frontal margin, separated from each other by a space narrower than frame of mouth-parts, each with a long slender seta. Anterior spiracles each with 1 or 2 trilocular disc pores; posterior spiracles without disc pores. Perivulvar disc pores in 5 groups; median group with 3 or 4 disc pores (dislocated from the body midline to the left side in all the four specimens, but shown on the midline in the accompanying figure); disc pores in each of antero- and posterolateral groups arranged in an elongate, double or often partly triple row, 10–13 in each anterolateral and 12–15 in each posterolateral group (8 in right posterolateral group in one specimen). Anus small, a little larger than a perivulvar disc pore, situated at centre of pygidium, superimposed on vulva or nearly so. Median trullae [median lobes] strongly convergent, fused together apically, leaving a notch between their apices [median notch], each trulla deeply notched once on slanting lateral margin; space between bases of median trullae with a small, oblong sclerosis; each trulla with a pair of slender linear scleroses arising from mesal and lateral basal corners and convergent anteriorly, the sclerosis arising from the mesal basal corner confluent with that of the opposite trulla in front of median notch; each of these scleroses succeeded by a strong rod-like sclerosis extending anteriorly, the lateral rod-like sclerosis especially strong, longer than the mesal, and swollen on anterior end, thus somewhat clavate. Second trullae represented by inner lobule alone, much smaller than median trullae but well represented, spiniform, strongly sclerotized, basally with a robust sclerotized area, which appears to be composed of a pair of scleroses. Marginal macroducts much elongated, slender but not filiform; 1 marginal macroduct opening just mesally to second trulla, the pore prominence associated with the orifice very slender, nearly needle-like; 2 laterally to second trulla, belonging to abd VI, their orifices associated with angulate sclerotized marginal processes; 1 on abd V, the orifice associated with a robust marginal process succeeded by smaller processes. Prepygidial dorsal macroducts also elongated, but shorter than marginal macroducts of pygidium, occurring in submedian and submarginal series along posterior margins of abd III and IV; submedian series with 1 or 2 macroducts on abd III and with 2 on IV; submarginal series with 6 or 7 macroducts on abd III and 4–6 on IV, the orifices set close, forming single rows. Lateral lobes of abd I and II with macroducts not particularly elongated, 3 or 4 on I and 1 or 2 on II. Ventral microducts scattered submedially on prepygidial abdomen. Abd I–III each with a tuft of

gland spines at apex of lateral lobe, 2 or 3 gland spines on I, 2–4 on II, and 2 or 3 on III; 1 or 2 marginal gland spines on abd IV well developed; 1 marginal gland spine on each of abd V–VIII. (No gland spines occur on the thorax, but in one specimen the metathorax bears a small gland spine on the digitiform process of the left side.)

Second-instar female, exuvial cast. Frontal margin flat. Pygidium similar to that in the adult female; marginal macroducts elongated, 2 on each side of pygidium, belonging to abd VI and VII; pore prominence on abd VII spiniform.

Remarks. This species is very similar to the other two leaf-associated species, *C. foliicola* and *C. palawanensis*, but differs from them mainly in the following characters of the adult female (characters in *C. foliicola* and *C. palawanensis* in brackets): Pygidium with lateral margins straight [concave subapically]; median trullae fused together apically [set close together, but not fused], notched once on lateral margin [minutely serrate]; sclerosis occurring between bases of median trullae oblong [shaped like an inverted U]; both abd III and IV with submedian and submarginal series of dorsal macroducts [abd IV without submedian dorsal macroducts]; lateral macroducts occurring only on abd I and II [occurring also on meso- and metathorax]; no gland spines on thorax (with an observed exception: see description above) [with gland spines on meso- and metathorax]. Furthermore, it differs from *C. foliicola* in having the anus situated at the centre of the pygidium [in *C. foliicola*, the anus is situated much posteriorly to the level of the vulva]. *C. glutae* is readily distinguishable from the other two known species of *Chionandaspis* in the state of the median trullae and the occurrence of elongate macroducts in both submedian and submarginal series on both third and fourth abdominal segments (in addition to the pattern of the marginal scleroses, which is similar among the leaf-associated species).

Discussion

Peculiar morphologies

The species assigned to the genus are commonly characterized in the adult female by the median trullae strongly convergent and having scleroses not only on their bases [basal scleroses] but also between their bases [median sclerosis], by the second trullae with the inner lobule alone well represented and provided with a strong sclerosis or a pair of scleroses basally, and by the marginal macroducts of the pygidium remarkably elongated or tending to be so. The basal scleroses of the median trullae are extraordinarily developed for chionaspidines in the four species except *C*. 91Kc-H, and in the type species those of both median and second trullae are quite unique in shape. Not only the marginal macroducts but also the submedian and submarginal macroducts are unusually elongated in the three leaf-associated species.

These characters may probably be associated with the burrowing habit of the females. In fact, elongated macroducts are found also in certain other burrowing chionaspidines (Takagi, 2003). Such macroducts, however, are not universal in burrowing forms of the Diaspidini. Remarkably developed scleroses on the pygidial apex are not commonly found in burrowing Diaspidini, either.

Morphoclinal analyses

The median trullae show rather slight differences among the species. In *C*. 91Kc-H and *C. ramicola* these trullae are separated from each other by a slender but distinct

slit; in *C. foliicola* and *C. palawanensis* these trullae nearly touch each other at their converging apices; in *C. glutae* they are fused together apically. These characters apparently form successive steps. The diaspidid pygidium is formed by a backward folding of some posterior segments of the abdomen, and the median trullae, situated at the posterior end of the pygidium thus formed, are interpreted to belong to the eighth abdominal segment; the space between the median trullae is deemed to represent the ninth segment, and its reduction can be an evolutionary trend. On this premise, the five species form a morphocline in the mentioned characters of the median trullae, and *C.* 91Kc-H and *C. ramicola* represent the primitive extreme of the cline: [*C.* 91Kc-H; *C. ramicola*] → [*C. foliicola*; *C. palawanensis*] → *C. glutae*.

The median trullae are minutely serrate except in *C. glutae,* in which these trullae are not serrate but only notched. Generally in burrowing scale insects, the median trullae and sometimes also the lateral trullae are elaborately serrate or dentate, and such trullae are supposed to saw the plant tissue when the insect body moves to burrow (Takagi, 2003). Simple (non-serrate) trullae, notched or not, are usual in non-burrowing diaspidids, and may be useful for cleaning the surface of the plant body for test formation. When these antipodal states of the trullae are applied to the morphocline mentioned above, the simple type in *C. glutae* is derivative in comparison with the serrate type in the other species. Because the simple type is common in non-burrowing diaspidids, the occurrence of this type in *C. glutae* appears to be contradictory. However, the median trullae in this species are fused together, and probably serve as a powerful tool for digging into the leaf epidermal layer. Burrowing starts in the second instar (as usual in burrowing diaspidids); the structure of the pygidial apex in the second-instar female is substantially the same as that in the adult female.

In the elongation of marginal macroducts, the five species show roughly successive steps: *C.* 91Kc-H → *C. ramicola* → [*C. follicola*; *C. palawanensis*; *C. glutae*]. In *C.* 91Kc-H only the mesal one of the marginal macroducts occurring on the sixth abdominal segment is evidently longer than the others; in *C. ramicola* most marginal macroducts are elongated; in the other species all the marginal macrodcuts are extraordinarily elongated and even the dorsal (submedian and submarginal) macroducts are also much elongated.

In the position of the anus relative to the level of the vulva the five species can be arranged in the sequence *C.* 91Kc-H → [*C. palawanensis*; *C. glutae*] → [*C. ramicola*; *C. foliicola*]. *C.* 91Kc-H, in which the anus is situated nearer to the base of the pygidium, may represent the primitive extreme. However, the polarity is not definitely determined and the significance of this sequence is left uncertain.

Ancestral form

The morphoclines mentioned above are not paradromic to each other, but *C.* 91Kc-H always appears at one extreme, which is relatively primitive or probably so. Other characters do not vary in succession through the five species, and there are gaps. A remarkable gap is found between *C.* 91Kc-H and the other species. *C.* 91Kc-H has simple scleroses associated with the trullae and a complete set of lateral macroducts and gland spines on the meso- and metathoarx and prepygidial abdominal segments. The other four species are provided with remarkably developed basal scleroses, which are extraordinary in size for chionaspidine scale insects and peculiar in shape, and lack lateral macroducts or both lateral macroducts and gland spines on one or more prepygidial segments, and in these characters they are obviously derivative in comparison with *C.* 91Kc-H, which,

thus, substantially represents a primitive form of the genus.

Further comparisons are uncertain as to their significance. The median sclerosis is quite conspicuous in *C*. 91Kc-H and much smaller in the other species; if the state in *C*. 91Kc-H is primitive in this genus, this sclerosis has reduced in size in the other species possibly in compensation for the remarkably developed basal scleroses of the trullae. The almost only possible derivative character of *C*. 91Kc-H, especially in comparison with the leaf-associated species, is the absence of submedian macroducts on the third abdominal segment, provided the decrease or loss of dorsal macroducts is an evolutionary trend in the genus (and generally in burrowing diaspidids). However, in general, the presence or absence of macroducts at a particular site may also occur as an infraspecific variation, and may not be worthy of serious consideration.

On the basis of the discussions above, *C*. 91Kc-H is regarded as representing or approximating a form ancestral to the other species of the genus.

The persistence of ancestral forms is expected from the gradistic view mentioned in Introduction. In another view, however, no relationships among contemporary organisms can be interpreted in terms of ancestral and descendant forms: the proposition that speciation always gives rise to two diverging species with their common ancestral species extinct at that moment is one of the basic tenets of 'phylogenetic systematics' or 'cladistics' (a school so called on its own interpretations of the terms 'phylogeny' and 'clade'). This proposition is effective methodologically as shown by an enormous amount of works made in the domain of this school, but this fact does not necessarily mean that the proposition is sound biologically. The punctuated equilibrium model explains phenomena observed in paleontological data and documented especially well in certain groups of animals: the discontinuity in rates of morphological change and the persistence of ancestral forms after giving rise to descendants (Eldredge and Gould, 1972; a recent revision: Gould, 2002). Neontological data are obtained from the end products of chronological events. When the punctuated equilibrium model represents a universal mode in evolution, there would be no good reason against applying ancestral-descendant relationship to morphoclinal and other morphological analyses in extant organisms.

Adaptive diversification

Another gap is found between the twig-inhabiting *C. ramicola* and the leaf-associated *C. foliicola*, *C. palawanensis*, and *C. glutae*, and thus suggests differentiation into advanced types in association with the feeding sites. The twig-associated type is characteristic especially in having the basal scleroses of the trullae uniquely shaped and in lacking dorsal macroducts on the prepygidial segments except for the presence of a few submarginal ones, and in these characters this type as compared with the leaf-associated type can be derivative. The leaf-associated type has the marginal scleroses well developed but less complicated in shape and the dorsal ducts occurring in submedian and submarginal series on the prepygidial abdomen. In these characters it is comparatively primitive, but it can be derivative in the extraordinarily elongated dorsal ducts. As discussed, *C. glutae*, belonging to this type, is the most derivative in having the median trullae fused together. In having different combinations of primitive and derivative characters, the twig- and leaf-associated types represent character patterns differentiated in adaptation to the burrowing mode of life on the twigs and on the leaves, both derived from the ancestral form represented by *C*. 91Kc-H, which occurs on the twigs.

Gaps: saltatory changes?

It is not knowable whether the gaps are attributable to intervenient forms that are unknown or extinct or to any saltatory events that might be involved. I do not deny the possibility of abrupt changes of phenotypic patterns in evolution. Needless to say, all morphologies are derived from growth phenomena, which at times may result in a drastic phenotypic change. In the Diaspididae, homomorphic and heteromorphic forms of the second-instar male, quite different in their character patterns, may occur in species that are very closely similar in the adult females and may be closely related, and therefore the change from one form to the other can be abrupt. Heteromorphic forms are atavistic in their general conformation, and their manifestation and suppression probably depend on some change in the genome caused by adaptive evolution in the adult female (Takagi, 2003). Potentiality of atavistic patterns held in the genome suggests potentiality of novel phenotypic patterns arising in the genome and their abrupt manifestation. However, whether the phenotypic change in the course of speciation is gradual or abrupt, whether it is teratological or not, and whether it is caused by gene mutation, alteration in gene expression, chromosome change, or genetic exchange (horizontal gene transfer; introgression; symbiogenesis; recombinational speciation), it should necessarily be exposed to adaptive selection, of which the pressure may greatly differ among ontogenetic stages according to life-historical and environmental conditions.

Concluding remarks

Chionandaspis as a whole is a peculiar genus in the subtribe Chionaspidina. The discussion above suggests that even a peculiar genus may originate with a less peculiar species and, once established, may promote adaptive speciation, apart from the question whether the emergence of its peculiar characters involves any peculiar process of evolution.

If the generalization stated above is correct, monotypic genera result, as a corollary, from their adherence to particular narrow niches or their failure to broaden their adaptive zones (niche-organism systems). Thus the problem of monotypic genera is concerned with the dimensions of the adaptive zones they exploit rather than with their morphological peculiarities or the mechanisms by which they emerge. New genera may arise through various mechanisms, but speciation in them should largely depend on the dimensions of the adaptive zones they exploit. Monotypic genera, if not arising by saltation, may be maintained by successively improved forms replacing the previous forms in restricted niches ('punctuated anagenesis': Gould, 2002), whereas other genera give rise to copious speciation in accordance with their broadened adaptive zones. According to Willmer (1990), the overall effect of evolutionary modes in the invertebrates is comparable to 'an old-fashioned meadow, where a few hardy perennial designs flourish and branch amongst the grasses'. Monotypic genera and speciose genera in a taxonomic group may compose a generic version of Willmer's meadow. Apart from their genealogical relationships, what they compose here should primarily be an adaptive-phenotypic landscape.

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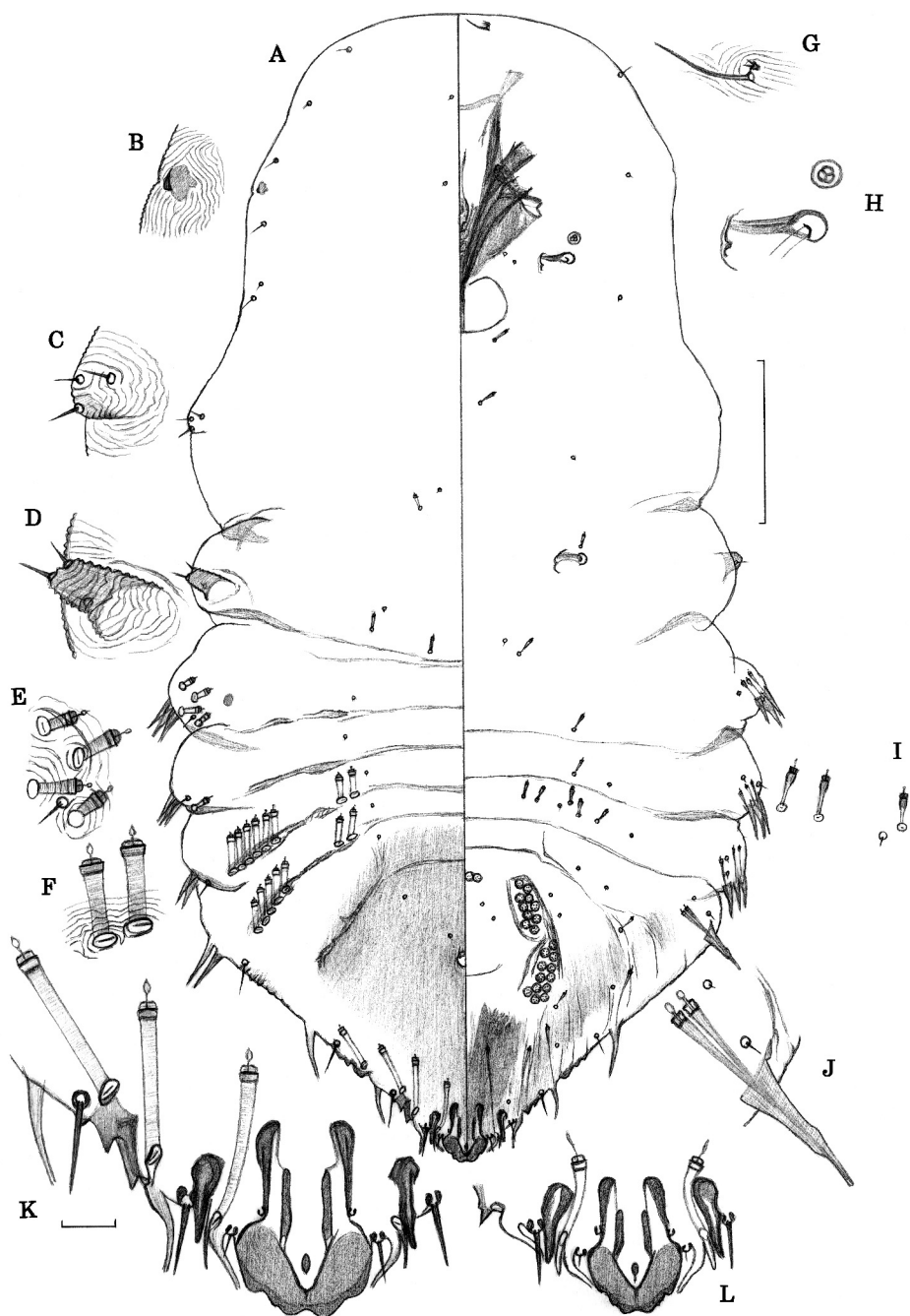
Chionandaspis glutae. A–K, adult female: B, eye-spot; C, lateral prominence on mesothorax; D, lateral digitiform prominence on metathorax; E, lateral macroducts on abd I [first abdominal segment]; F, submedian dorsal macroducts on abd III; G, antenna; H, anterior spiracle; I, submedian ventral microducts on abd III; J, marginal gland spine on abd IV; K, apex of pygidium, dorsal surface. L, exuvial cast of second-instar female: apex of pygidium. Scale bars: A, 100μm; K, 10μm (B–J and L magnified at the same rate as K).